

CANNIBALISM IN REPTILES: A WORLDWIDE REVIEW



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SOCIETY FOR THE STUDY OF AMPHIBIANS AND REPTILES

Herpetological Circular No.15

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Frontpiece: *Lampropeltis getulus* - California king
snake eating a newborn conspecific.
by TOM R. JOHNSON

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**By
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1986

ACKNOWLEDGEMENTS

My review of the reptilian literature would not have been possible without the help of the libraries and the librarians of the following institutions: University of Richmond, Smithsonian Institution, University of Tennessee, and Virginia Commonwealth University. Katherine E. R. Smith and Betty B. Tobias (University of Richmond) were particularly helpful and were able to locate even the most obscure reference. I am also grateful to the following individuals who contributed and/or helped to locate references: I. S. Darevsky, J. Davis, H. W. Greene, R. E. Honegger, J. B. Iverson, D. R. Jackson, P. E. Vanzolini, A. H. Wynn, G. R. Zug, and R. G. Zweifel. Christopher A. Pague, Vicki B. Roy and Joseph C. Troncale assisted with translations.

I am grateful to the following people who contributed original observations and waited patiently for them to be published: S. J. Arnold, D. G. Broadley, G. Carl, K. A. Christian, W. B. Cove, C. M. Craig, R. I. Crombie, I. S. Darevsky, R. E. Honegger, W. W. Lamar, J. Lewis, M. J. Miller, H. K. Nettmann, M. C. Nowak, C. R. Peterson, H. Quinn, M. D. Robinson, S. Rykena, L. M. Scudder, H. L. Snell, J. W. Steiner, J. Stout, S. N. Trautwein, and L. J. Vitt.

The manuscript benefited from the criticisms of D. G. Broadley, C. Gans, R. E. Honegger, B. Lanza, P. E. Vanzolini, G. R. Zug and an anonymous reviewer.

My wife, Wendy H. Mitchell, participated in all phases of this review. I am grateful to her for helping with translations, literature search and proof-reading, and for her untiring support and encouragement.

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INTRODUCTION

Cannibalism in reptiles has been known for several centuries (Banta, 1974) but was first recorded in the scientific literature in the late 1800's. Stejneger (1893) noted that leopard lizards (*Gambelia wislizenii*) consumed members of their own kind. A year later Bartlett (1894) published an observation on a *Boa constrictor* consuming a conspecific adult in the London Zoo. An early report in the popular literature (Anonymous, 1892) briefly described cannibalism in captive kingsnakes and watersnakes. Since then, there has been a variety of reports of cannibalism in reptiles, ranging from a brief statement of its occurrence in a particular species to detailed descriptions. The literature, however, has never been adequately reviewed.

That cannibalism is a natural behavioral phenomenon beneficial to some members of a population, and thus subject to natural selection, was demonstrated by Fox (1975). In his review, Fox briefly mentioned amphibians, specifically anurans, but did not refer to reptiles. Cannibalism is well known in some invertebrates, birds, mammals, fish and amphibians (Fox, 1975; Eisenberg, 1981; Polis, 1981; Polis, et al., 1984; Dionne, 1985; Mock, 1985; Polis and Myers, 1985), but has been examined only recently in reptiles. Hermann (1921) presented a number of cases of ophiophagy in snakes but in only two species was true cannibalism observed. He concluded that the event occurs only rarely. Petzold (1982) listed 16 species of cannibalistic reptiles in his review of problems in captive husbandry. He discussed cannibalism from the perspectives of overcrowding and, particularly for snakes, the consumption of one by another when both were eating the same prey item. More recently, Polis and Myers (1985) summarized instances of cannibalism in forty species of reptiles. Based on the apparent lack of explanations for reptilian cannibalism in the literature and the high frequency of juveniles consumed, they concluded that cannibalism in reptiles is "purely opportunistic predation". My review shows that both of these premises are false and that this conclusion was premature.

The past and present literature reveals inconsistencies and problems with terminology relating to cannibalism. This paper presents a review of the literature and a discussion of the terminology and problems. It also includes new records for many species and recommendations for future reports on cannibalism in reptiles.

TERMINOLOGY, DEFINITIONS AND CORRECTIONS

The term "cannibalism" has been used correctly and incorrectly from the earliest literature accounts to recent communications on the subject. Cannibalism is applicable only in cases of intraspecific predation (Fox, 1975; McNicholl, 1977; Polis, 1980, 1981; Polis and Myers, 1985). Wall (1904) considered 12 cases of one snake consuming another to be cannibalism, but in only one of the cases was the term correctly applied. As late as the early 1970's cannibalism was used to describe observations of interspecific predation in snakes (Soderberg, 1971). "Cannibalism" was incorrectly applied in papers by Rao (1924), Ditmars (1929, 1936), Greenhall (1936), Fleay (1941) and Dias, et al. (1961). Broadley (pers. comm.) suggested that FitzSimons (1962) confused cannibalism with ophiophagy for *Mehelya capensis*.

As McNicholl (1977) pointed out, cannibalism has been used in two ways: 1) the eating of a dead conspecific, and 2) the killing and eating of a conspecific. In many of the reports on reptiles there is insufficient information to determine if the "victim" had died by means other than as a result of the cannibal's behavior. Where possible in the species accounts, however, I indicate whether the victim was dead or was known to have been killed before consumption. Terms, such as infanticide and sibicide used for birds and mammals, are not encountered in the herpetological literature because reptiles usually eat what they kill. That is not the case with homeotherms (Eisenberg, 1981; Polis, et al., 1984; Mock, 1985). Kronism (parents killing offspring) has been used in one reference to reptiles (Auffenberg, 1981).

The behavioral acts of autophagy and oophagy often have been called cannibalism (e.g., Heimlich and Heimlich, 1947; Martof, 1956; Fitch and Henderson, 1978; Christian and Tracy, 1982). However, these are specialized behaviors not involving predation and consumption of conspecific individuals. Autophagy is the consumption of a part of one's own body and is most often used in description of lizard behavior where tail consumption follows its autotomy. Tail autotomy is well known in lizards and the consumption of lizards' own tails is well documented (Grant, 1957; Clark, 1971; Vitt, et al., 1977). Oophagy refers to the consumption of eggs or embryos by a conspecific (intraspecific oophagy) and the eating of eggs of other vertebrate species (interspecific oophagy). I have chosen to separate intraspecific oophagy from my treatment of cannibalism here because it is a specialized behavior involving different stimuli and occurs most often in female reptiles eating their own eggs or embryos. The literature on intraspecific oophagy and autophagy is extensive (Mitchell, unpublished) and is not included here.

There are several errors and misrepresentations in Table 1 of Polis and Myers (1985). Of the forty species listed, three (*Elaphe scalaris*, *Gopherus agassizii*, *Lacerta lepida*) were included because the "victims" were eggs. Six references listed are not the original descriptions, but refer to the cannibalistic event described in other papers. These are *Gopherus agassizii* (reference 29), *Anolis lineatopis* (73), *Sceloporus magister* (36), *Sceloporus chrysostictus* (36), *Crotaphytus collaris* (30), *Leptodeira annulata* (66), and *Bitis arietans* (10). Reference 77 for *Sceloporus graciosus* and *S. occidentalis* includes "Sceloporus hatchlings" as prey for both species. However, it is not possible to ascertain which species consumed which. The reference for *Sceloporus woodi* is listed incorrectly as 86; it should be number 6. Reference 6 is incorrectly included in the list for *Uta stansburiana*. Reference 61 was left out of the list for *Agkistrodon contortrix*. The reference for cannibalism in *Moloch horridus* (67) contains no such information and reference 30 for *Gambelia* (*Crotaphytus*) *wislizenii* contains no mention of cannibalism for this species. Lastly, twelve references (6, 10, 19, 23, 24, 29, 46, 47, 51, 61, 65, 95) contain information not included in Polis and Myers (1985) on predator and prey size data and whether the event took place in captivity or in the field.

DISCUSSION

A total of 191 species of reptiles is reported to have exhibited cannibalism: 39% lizards, 53% snakes, 4% turtles and 4% crocodilians. Lizards are represented by ten of the 17 families listed in Duellman (1979). Five families of snakes are represented, as are five families of turtles. The only living family of crocodilians is represented by seven species. No instances of cannibalism are known for amphisbaenians (C. Gans, pers. comm.; this study) nor for the tuatara.

There are no apparent trends or strong associations in comparisons among families, ecological adaptations, or evolutionary relationships. Twice as many observations (= literature references) of cannibalism in lizards were made in the field (60) than in captivity (32). The opposite relationship holds for snakes, 60 field versus 106 in captivity. This probably reflects the difficulty of observing behavioral events with snakes in the field, and the reporting of single events in the snake literature. There may be a true biological basis for the difference, however. Captive and field observations were about equally divided in turtles and crocodilians.

In eighteen reports, the victim was known to have been killed by the cannibal before consumption, and in eleven reports the victim was already dead. These latter cases are more properly termed carrion eating

(McNicholl, 1977) or, more precisely, intraspecific carrion eating. In lizards only *Varanus komodoensis* is known to consume dead conspecifics (Auffenberg, 1980, 1981). Seven species of snakes have been reported to eat conspecific carrion: *Agkistrodon contortrix* (Mitchell, 1977), *A. piscivorus* (Smith and List, 1955), *Crotalus viridis* (Gloyd, 1933; Powers, 1972; Lillywhite, 1982), *Crotaphopeltis hotamboeia* (Rose, 1962), *Dispholidus typus* (Rose, 1954), *Epicrates striatus* (Huff, 1980), and *Sistrurus catenatus* (Ruthven, 1911). A special case of cannibalism occurs when two conspecific snakes attempt to eat the same prey item and results in one, usually the larger, swallowing the other. This event was recorded nineteen times and all but two (in *Micrurus fulvius*) occurred in captivity. This behavior is doubtless more widespread than has been reported, but captive snakes are usually separated before the death and consumption of the victim.

The occurrence of a cannibalistic event in which one conspecific kills another before consumption suggests that normal conspecific recognition signals and/or responses have malfunctioned. Visual recognition of adults by conspecific adults is known in some lizards (Glinski and Kjekshus, 1985). Studies by Bissinger and Simon (1981), Cooper and Vitt (1984a,b), Duvall (1979), Duvall, et al. (1980), Ford and Schofield (1984), Simon, et al. (1981) and others have shown that chemoreception is also used in recognition of lizard and snake conspecifics. Cannibalistic individuals may be unable to detect conspecifics visually or chemically because of physiological or neurological defects. There may be genetic basis for these defects. In such individuals visual or chemical stimuli may result in a predatory response. Conversely, an individual being cannibalized may be unable to perform the correct species-specific behavioral sequence or produce the pheromones which stimulate conspecific recognition.

The special case of two snakes engulfing the same prey item resulting in one consuming the other could occur for two reasons. Increased levels of "excitement" during feeding, i.e., feeding frenzies, may mask normal recognition responses and, combined with prey odors present on the heads of both snakes, could result in consumption of the entire prey package (prey and second snake). In addition, detection of conspecific pheromones is probably limited while tongue protrusion is blocked by the prey in the snake's mouth. Gans (1952) noted that, once feeding starts, snakes will consume subsequent prey items indiscriminately until the supply stops and that they will grab any object of appropriate size, shape and color. Perhaps the feeding response is stronger than responses to conspecific cues.

In lizards, recognition of conspecific juveniles by adults may be less refined than adult-adult recognition. Fifty-eight of the 106 reports of cannibalism in lizards noted that adults consumed juveniles. Of those, 31% occurred in captivity and 69% occurred in the field. Juveniles may not perform adult visual displays and, in large enclosures or in the field, may signal

a predatory response based on movements well before chemoreception stimulates a recognition response. The presence of color and pattern differences between adults and juveniles may be the result of natural selection for avoidance of cannibalism. Rand and Andrews (1975) suggested this to explain pattern differences in *Anolis cuvieri*. They experimentally demonstrated that adults avoided eating juveniles, possibly because of their recognition of the juvenile pattern.

A number of ecological and evolutionary benefits accrues from cannibalism. These are adequately reviewed by Fox (1975) and Polis (1980, 1981). A few of them should be mentioned, however. Cannibalism may act as a density-dependent regulating mechanism in some populations. While there is no evidence that high population densities contribute to snake cannibalism, it may be a factor in lizards and crocodilians. This consequence has been suggested for reptiles, especially lizards, by Fitch (1963), Badir (1968), Frye (1973), Auffenberg (1981), Petzold (1982) and M.L. Robinson (pers. comm.). In an experimental density study, Tubbs and Ferguson (1976) observed increased aggression, chasing and biting of conspecific *Sceloporus*, but no cannibalism. They suggested that a General Adaptation Syndrome (GAS), as known for mammals, may result from overcrowding. In addition to decreased movement and feeding, slower growth rates and lower survivorship in subordinates (Tubbs and Ferguson, 1976), GAS could affect production of conspecific pheromones and alter recognition behaviors. This, coupled with increased hunger levels in overcrowded populations, could induce cannibalistic behavior. Giese (1973, in Polis, 1980) coined the term "lifeboat strategy" to describe a means of avoiding extinction. Briefly, cannibals in cannibalistic populations could survive periods of resource deprivation, whereas populations without cannibals would become extinct. Only Auffenberg's (1981) study of *Varanus komodoensis* suggests the lifeboat strategy may be employed by reptiles. Cannibalism may provide evolutionary benefits for individuals. These include potentially faster growth rates, higher survivorship, larger size, higher probability of mating, and increased fitness. Competition between siblings, relatives, mating rivals, and others in the population may be reduced by cannibalistic individuals. Fox (1975) and Polis (1981) review these consequences for a host of organisms. The occurrence and consequences of these benefits in natural populations of reptiles are unknown. Research focusing on ecological and evolutionary benefits for reptiles is likely to be long-term. Wilson (1975) noted that cannibalism was recorded at higher frequencies when field studies exceeded 1000 hours in duration. This may be more due to the extended observation time than to observer influence.

Is cannibalism in reptiles purely opportunistic predation? Polis and Myers (1985) base their conclusions on the high incidence (16 of 18) of adults consuming juveniles and the lack of speculation on causes in the literature they reviewed. My review of the literature demonstrates that the frequency

of adult-juvenile cannibalism is high only for lizards and that most of the recorded events occurred under natural conditions. It might be expected that this frequency would have a positive relationship with population density. Badir (1968) demonstrated this in experimental density manipulations of *Chalcides ocellatus* populations. Higher rates of cannibalism may occur in any euryphagic lizard when exposed to very high densities in laboratory or field enclosures. Furthermore, intraspecific predation should occur more often by adults on juveniles because of size considerations and because of chemosensory and behavior problems noted above. Experiments in which juvenile behavior, chemosensory recognition, and hunger, as well as population densities, are manipulated may determine which factors are the most important in causing cannibalism. While it may be difficult to conduct such experiments on crocodilians due to their conservation status, the observations by Staton and Dixon (1975) on *Caiman crocodilus* suggest the frequency of cannibalism in these animals may also be related to unusually high population densities. For turtles, only Chen (1976) has noted that *Trionyx sinensis* adults cannibalize juveniles under, apparently, high population densities. Density manipulation in aquaculture ponds could address the question of frequency. However, turtles would have to be housed in the laboratory to determine if behavioral or olfactory differences contribute to cannibalism. Experimental manipulations of snake population densities would probably produce similar results to those on lizards, especially if euryphagous species, such as *Coluber constrictor*, were used. Compared to lizards, however, snakes are more stenophagic. The lack of evidence suggesting density-dependent cannibalism is more likely related to this and the fact that most snake predation events are witnessed in captivity rather than in the field. For most snakes, the elucidation of the causes of cannibalistic behavior via manipulation of chemosensory recognition and signal cues would seem to be a fruitful approach. Why doesn't a snake recognize that a conspecific is attached to the other end of the mouse? Speculations above are only just that. This brief review demonstrates that there is justification for suggesting density-dependent cannibalism in some cases and that there have been such suggestions in the previous literature. Thus, the conclusion by Polis and Myers (1985) that all reptile cannibalism is purely opportunistic predation was premature. While that may be the best explanation in some instances, it certainly does not explain the causes of cannibalism in all reptiles.

Finally, the evolution of cannibalism in reptiles can be viewed from two perspectives. Cannibalism can increase an individual's reproductive success (fitness) by providing a source of food at times of reduced resource levels and by serving as a source of mortality for potential competitors. If this behavior has a genetic basis, it could be acted upon by natural selection under certain environmental conditions. Cannibalism could also occur as a by-product of a separate and more strongly selected behavior, such as the feeding response, which, when over-stimulated causes can-

nibalistic behavior. This could explain why cannibalism may occur in feeding frenzies and why one snake engulfs another when both try to consume the same prey item. In this sense, cannibalism may not be a behavior which can be acted upon by natural selection. The anecdotal evidence suggests that natural selection is more likely to be operative for lizards and crocodilians than for snakes.

CONCLUSIONS

Cannibalism is not rare in reptiles. For most individual species, however, the event appears to occur infrequently. Most known accounts are anecdotal and do not provide insights into the causes and consequences of this behavior. Conditions of captivity may be a factor in inducing cannibalism in many species, especially snakes. Research with lizards provides the most promising opportunities for elucidating some of the relationships of cannibalism with population densities. Research on this and other aspects of cannibalistic behavior is certainly worth pursuing.

Reports of cannibalism should be published, but should include the following points: 1) whether the victim was dead before consumption (i.e., carrion) or if it was killed by the cannibal; 2) sizes and sexes of the individuals; 3) description of the circumstances leading to the events, including whether the event took place in captivity or under natural conditions; and 4) behaviors of the cannibal and victim before, during, and after the event. Information on population density and resource levels would help to elucidate whether ecological conditions contributed to the cannibalistic event.

Species Accounts

For many species listed below the information available is placed in an abbreviated format. In each of these I note the relative size of the predator and prey (adult-adult, adult-juvenile, or juvenile-juvenile, respectively) and whether the observation was made in the field or if it occurred in captivity. "Field" also refers to the discovery of a conspecific in stomachs of field-collected specimens. Where possible, the sex of the individuals is noted. A question mark indicates the information provided in the source only suggested a captive or field occurrence. Notations of "no specific information" or "unknown" indicate cannibalism was mentioned for the species but the reference contained no other information. References follow each notation. In many cases the information is summarized and in others complete descriptions are provided in paragraph form. Accounts and descriptions providing sex and size data, ecological information or behavioral notes are presented in this fashion. Species are listed in alphabetical order by genus within their Order or Suborder.

Sauria

Acanthodactylus pannonicus - no specific information, field: Bogdanov (1965).

Acanthodactylus erythrurus - no specific information, field: Busack and Jaksic (1982).

Acanthodactylus schreiberi - adult-juv., unknown: Werner (1952).

Agama agama - adult-juv., field(?): Cansdale (1955); no specific information, unknown: Cloudsley-Thompson (1981).

Agama caucasia - no specific information, unknown: Ataev (1985).

Agama sanguinolenta - no specific information, unknown: Ataev (1985).

Anguis fragilis - juv.-juv., in captivity: Petzold (1971). Davies (1967) noted that a captive female ate two of her offspring to which she had just given birth.

Anolis lineatopus - Rand (1967) observed a 60 mm SVL male catch and eat a 20 mm juvenile in the field. He also found a hatchling in the stomach of an adult.

Anolis poecilopus - adult-juv., field: Campbell (1973).

Anolis roquet - no specific information, probably field: Schoener and Gorman (1968).

Aporosara anchietai - In field-collected specimens, Robinson and Cunningham (1978) found an entire hatchling and the tail of another in stomachs of two adult males, respectively. Michael D. Robinson (pers. comm.) noted this behavior may be related to the greater than average densities during December and January in the Namib Desert.

Chalcides ocellatus - Badir (1968) established two densities of lizards in terraria, one per 400 cm² surface area and one per 26.1 cm². Compared to low density lizards, high density lizards exhibited more aggression, embryonic mortality up to 86% per female and cannibalism of neonates by adults of (apparently) both sexes.

Cnemidophorus inornatus - no specific information, field: Milstead (1957).

Cnemidophorus sexlineatus - A field-collected adult male contained a 27 mm SVL juvenile swallowed headfirst (Etheridge and Wit, 1982).

Cnemidophorus tigris - adult-juv., field: Mitchell (1979); adult-juv., field: L. J. Vitt (pers. comm.).

Corucia zebrata - juv.-juv., in captivity: Honegger (1985).

Crotaphytus collaris - adult-juv., unknown: Ellis and Henderson (1913); adult-juv., unknown: Burt (1928); adult-juv., field: Smith (1946); adult-juv., field(?): Shaw (1950); adult-juv., in captivity: Mosley (1963).

Ctenosaura similis - adult-juv., field: Fitch and Henderson (1978).

Cyclura carinata - Iverson (1979) found a juvenile in the stomach of a field-collected adult and observed another adult capture and consume a juvenile conspecific. Auffenburg (1982) found a hatchling in a 203 mm SVL female.

Dipsosaurus dorsalis - no specific information, field: Norris (1953).

Egernia cunninghamii - adult-juv., in captivity: Honegger and Schmidt (1964).

Elgaria multicarinata - adult-adult, field and in captivity: Cunningham (1956). Gander (1934) noted that a 121 mm SVL female ate an 80 mm cagemate. John Davis (pers. comm.) observed an approximately 203 mm (total length) adult stalk, capture, kill and eat an approximately 89 mm (total length) juvenile in the field. Handling time was about 18 minutes.

Eremias nikolskii - no specific information, field: Bogdanov (1965).

Eremias persica - no specific information, unknown: Ataev (1985).

Eremias velox - no specific information, field: Bogdanov (1965).

Eumeces fasciatus - Fitch (1954) found two hatchlings in stomachs of field-caught adults.

Eumeces septentrionalis - A field-collected adult female was found to contain a young conspecific in her stomach (Breckenridge, 1943).

Eumeces skiltonianus - no specific information, in captivity: Zweifel (1952).

Eumeces laticeps - adult-adult, in captivity: M. C. Nowak (pers. comm.). Douglas (1965) mentions the consumption of a small female by a large male in captivity.

Gambelia wislizenii - adult-adult, field: Stejneger (1893); adult-adult, field: Van Denburgh (1922); no specific information, unknown: Smith (1946); adult-juv., field: Montanucci (1965). Montanucci (1967) observed that the greatest number of cannibalistic events occurred in spring (April-May); most stomachs containing conspecifics had juveniles of ≤ 75 mm SVL.

Gecko gekko - adult-juv., in captivity: Dollinger (1971).

Hemidactylus flaviviridis - adult-juv., in captivity: Mahendra (1936).

Holbrookia propinqua - Judd (1976) reported that two field-collected adults contained parts of juveniles in their stomachs.

Lacerta agilis - adult-juv., in captivity: Street (1979).

Lacerta lepida - adult-juv., in captivity: Laferriere (1970).

Lacerta muralis - adult male-juv., field: Kabisch and Englemann (1969).

Lacerta strigata - no specific information, field (?): I. S. Darevsky (pers. comm.).

Lacerta trilineata - no specific information, field (?): Bannikov, et al. (1977).

Lacerta viridis - no specific information, field (?): Bannikov, et al. (1977).

Leposoma parietale - Duellman (1978) noted that one field-caught specimen contained a head of a juvenile.

Lialis burtonis - no specific information, in captivity: Mackay (1960).

Lygosoma metallicum - no specific information, in captivity: M. Miller (pers. comm.).

Mabuya aurata - no specific information, unknown: Ataev (1985).

Mabuya striata - adult-juv., in captivity: D. G. Broadley (pers. comm.).

Neusticurus ecpleopus - Duellman (1978) reported that three field-collected specimens contained conspecifics in their stomachs.

Ophisaurus apodus - no specific information, field (?): I. S. Darevsky (pers. comm.).

Ophisaurus ventralis - Carr (1940) mentioned that captive specimens were cannibalistic. Hamilton and Pollack (1961) found five specimens in the field with remains of conspecifics in their stomachs.

Phrynocephalus mystaceus - no specific information, unknown: Ataev (1985).

Phrynosoma douglassi - adult-juv., field(?): Dodge (1938); adult-juv., field (?): Smith (1946).

Ptychozoon kuhlii - adult-juv., in captivity: M. J. Miller (pers. comm.).

Podarcis muralis - Kabisch and Engelmann (1969) found a juvenile in the stomach of a field-collected adult.

Pygopus lepidopodus - no specific information, in captivity: Mackay (1960).

Rhacodactylus leachianus - adult-juv., in captivity: Dollinger (1971).

Rhacodactylus trachyrhynchus - juv.-juv., in captivity: Bartmann and Minuth (1979).

Sceloporus chrysostictus - Smith and Fritts (1969) noted that a field-collected 55 mm SVL male contained a 22 mm male in its stomach.

Sceloporus graciosus - no specific information, field: Knowlton (1934).

Sceloporus jarrovi - no specific information, field: Smith (1946).

Sceloporus magister - adult-juv., field: Knowlton and Thomas (1934); adult-juv., field: Tanner and Krogh (1973).

Sceloporus occidentalis - of ten specimens placed in a cage together, four were consumed by larger individuals (Skehan, 1960). In a field study of 210 specimens, three juveniles had been consumed by as many adults (Johnson, 1965).

Sceloporus olivaceus - adult-juv., in captivity: Kennedy (1956).

Sceloporus orcutti - Mayhew (1963) found a 39 mm SVL juvenile in an 81 mm field-collected male.

Sceloporus torquatus - Staton and Conzelmann (1975) found a 30 mm SVL juvenile in a 79 mm female and speculated that she may have been par-turient and had eaten one of her own offspring.

Sceloporus undulatus - adult-juv., in captivity: S. N. Trautwein (pers. comm.). Groves (1971) reported the consumption of a 24 mm SVL juvenile by a 52 mm captive male.

Sceloporus woodi - A 30 mm SVL juvenile was found in the stomach of a 53 mm field-collected female (Bowie, 1973).

Scincella lateralis - Lewis (1951) noted that a large captive female ate five neonates of a conspecific female. Duvall, et al. (1980) reported that pieces of "ground skink" (probably tails and legs) have been observed in terraria containing laboratory populations.

Tropidurus albemarlensis - H. L. Snell (pers. comm.) reported an observation on Fernandina Island of a male that grabbed a female and tried to mount her but ate her instead. He has also seen adults eating conspecific hatchlings and juveniles.

Tropidurus habeli - Carpenter (1970) noted that an adult male captured and ate a conspecific juvenile in the field.

Uma notata - adult-juv., in captivity: Shaw (1950); adult-juv., field: Carpenter (1963). Sugerman and Applegarth (1980) found a 51 mm SVL juvenile swallowed headfirst in the stomach of a 100 mm male that had been bitten and killed by a sidewinder.

Urosaurus graciosus - adult-juv., field: Vitt and Ohmart (1975).

Uta stansburiana - adult-juv., field: Knowlton and Jones (1933); adult-juv., field (?): Smith (1946); adult-juv., field: Tinkle (1967).

Varanus gouldii - Johnson (1976) reported that, after a month in captivity, an adult 910 mm SVL male attacked a 382 mm juvenile, "killed it, tore it to pieces, and devoured it". King and Green (1979) found the remains of a small *V. g. rosenbergi* in a field-collected specimen. They were unable to ascertain whether the prey was killed before consumption or if it was consumed as carrion.

Varanus griseus - no specific information, unknown: Flower (1933); no specific information, field: Bogdanov (1965); adult-juv., unknown: Gerlach (1971); adult-juv., field: Vernet and Grenot (1972).

Varanus komodoensis - Burden (1928) reported komodo monitors will eat rotting meat of conspecifics and will kill and eat a wounded member of the population. He found no evidence that larger ones hunt and kill small ones. Auffenberg (1970, 1980) mentioned that small monitors are eaten by larger ones and that 66 occurrences of cannibalism were found in an analysis of 4267 scats. In his book (Auffenberg, 1981), he includes considerable information on cannibalistic behavior, its prevalence, and sizes of cannibals and victims. Briefly, cannibalism is practiced by medium to large-sized lizards, accounts for 2.2% to 8.8% of total food items, and occurs mostly on small lizards. Some old, large lizards are sometimes eaten

but their consumption probably results from scavenging (Auffenberg, 1981), although a few were killed and eaten. Frequency of cannibalism is higher during periods of high population density and probably plays a role in density regulation.

Varanus storri - Peters (1973) stated that this species, along with other varanids, has cannibalistic tendencies. He suggested that cannibalism may explain the absence of juveniles.

Xenosaurus grandis grandis x rackhami - Captive adults of both sexes readily consume neonates: (Campbell, Lamar, and Murphy, in prep.) W.W. Lamar (pers. comm.)

Serpentes

Agkistrodon contortrix - Mitchell (1977) reported the consumption of a dead neonate by a 227 mm SVL captive littermate; consumption time was about 2 hours. Harris and Simmons (1977) noted that a captive 760 mm adult regurgitated a 610 mm cagemate.

Agkistrodon halys - no specific information, field: Bogdanov (1965).

Agkistrodon piscivorus - adult-juv., field: Penn (1943); no specific information, unknown: Allen and Swindell (1948); adult-juv., field: Klimstra (1959); no specific information, in captivity: Petzold and Engelmann (1975); no specific information, in captivity: Neill (1968); adult-juv., in captivity: C. M. Craig, (pers. comm.); adult-juv., field: M. C. Nowak (pers. comm.). Conant (1934) noted that a captive cottonmouth killed and ate a smaller conspecific. Smith and List (1955) noted that a field-captured specimen regurgitated a decapitated conspecific. Burkett (1966) reported that two of 46 field-caught specimens contained other cottonmouths.

Aspidelaps lubricus - no specific information, in captivity: J. Lewis (pers. comm.).

Atheris squamiger - adult-adult, in captivity: Wallach (1980).

Atheris superciliaris - adult-adult, juv.-juv., in captivity: Stevens (1973).

Atractaspis bibronii - FitzSimons (1962) noted this species has "distinct cannibalistic leanings" and preys on quite a variety of different snakes.

Austrelaps superbus - Shine (1977) recorded that one of 26 field-caught specimens contained a conspecific.

Bitis arietans - FitzSimons (1932) contains a photograph of a captive individual which had swallowed a conspecific.

Bitis gabonica - adult-juv., in captivity: Pitman (1974).

Bitis schneideri - Haacke (1975) noted that one specimen contained the remains of a small adder "probably of its own kind".

Boa constrictor - In the London Zoo, an 11 foot boa ate a 9 foot conspecific (Bartlett, 1894), but no other details were provided. Six instances of cannibalism were noted at the Zurich Zoo (R. E. Honegger, pers. comm.) between 1974 and 1981. All involved juveniles of the same ages and only one resulted from two snakes eating the same prey item.

Boiga cyanea - adult-adult, in captivity: Vit (1976). Smith and Kloss (1915) reported an apparently field-caught 1260 mm (total length?) male which contained a 1350 mm female.

Bothrops jararaca- juv.-juv., in captivity: Hermann (1921), noted as *B. lanceolatus*.

Bothrops nasuta - juv.-juv., in captivity(?): Picado (1931, 1976); adult-adult, juv.-juv., in captivity: Porras, et al. (1981).

Bothrops nigroviridis - a 762 mm female ate a 508 mm male with which it had been caged for three years: H. Quinn (pers. comm.).

Bothrops schlegeli - adult female-adult male, in captivity: H. Quinn (pers. comm.).

Bungarus caeruleus - no specific information, unknown: Wall (1906); no specific information, in captivity: Whitaker (1978). A field-caught 118 cm (total length) female had swallowed a 99 cm female headfirst after apparently killing her (Smith, 1914). Dattatri (1984) found a 123 cm total length male containing a 90 cm total length gravid female he had swallowed head first.

Bungarus multicinctus - adult-juv., field: Mao (1970).

Calloselasma rhodostoma - juv.-juv., littermates, in captivity: Blody (1983).

Charina bottae - Peabody, et al. (1975) described the behavior of a captive juvenile (251 mm total length) which escaped ingestion from an adult male (488 mm) by constricting him and pulling its head out. This occurred five times and in each case, the snakes were engulfing the same prey item. Prior to these events a 580 mm female had swallowed 75% of the male alive.

Chilorhinophis gerardi - a 460 mm total length adult female swallowed an adult male in captivity (Broadley and Cock, 1975; D.G. Broadley, pers. comm.).

Chondropython viridis - a 1977 photograph shows a juvenile regurgitating a partially consumed littermate (Gray, 1977).

Clelia clelia - adult-adult, in captivity: Dollinger (1971).

Coluber constrictor - adult-juv., field: Conant (1938); juv.-juv., in captivity: Liner (1949); no specific information, field: Hamilton and Pollack (1956); no specific information, in captivity: Cunningham (1959); no specific information, field: deRageot (1964). Of 1357 food records for *C. constrictor*, 18 were conspecifics and 14 of these were juveniles (Fitch, 1963). He noted that cannibalism may be a significant factor in the population dynamics of yearlings. Fitch (1982) reported 16 conspecifics in racer stomachs. In a field study in Georgia, one of 54 racers with full stomachs contained a juvenile (Duever, 1967). Jackson (1971) reported a natural predation event in which a 1020 mm total length adult actively searched for, caught and ate a 520 mm juvenile in leaf litter. Brown (1979) observed a 1000 mm total length male "vigorously swallowing" a 500 mm male in the field.

Coluber viridiflavus — no specific information, unknown: Street (1979). Naulleau (1973b, 1984) recorded a 1300 mm (total length) male which had swallowed a 600 mm juvenile male; apparently both tried to swallow the same prey item.

Coniophanes fissidens - no specific information, field: Seib (1985).

Coronella austriaca - no specific information, unknown: Street (1979); adult-adult, adult-juv., in captivity: Gerlach (1971).

Coronella girondica - no specific information, unknown: Angel (1946); adult-juv., in captivity: Stemmler (1980).

Crotalus atrox - juv.-juv., in captivity: Klauber (1972).

Crotalus cerastes - Funk (1965) reported that a 590 mm SVL field-caught adult had eaten a 223 mm conspecific.

Crotalus lepidus - Williamson (1971) reported the consumption of a captive juvenile by a litter mate which itself was subsequently eaten by the adult female. Harris and Simmons (1977) mentioned a 530 mm captive male *C. l. klauberi* eating a "thin" female conspecific.

Crotalus mitchelli - Porter (1983) reported that one individual *C. m. stephensi* x *pyrrhus* apparently killed and ate a conspecific littermate when it was returned to the holding cage after being fed a dead, "ripe" mouse. The cannibal subsequently ate two other conspecifics. All victims were regurgitated.

Crotalus viridis - Gloyd (1933) noted that a field-caught specimen disgorged a conspecific which was apparently dead when eaten. Hathcock (1937) included a photograph of an adult eating a conspecific adult in captivity. Cunningham (1959) mentioned that a captive adult ate a juvenile when both tried to eat a mouse. A captive adult *C. v. helleri* introduced into a cage containing an adult conspecific was consumed two days later (Cardwell, 1964). Bullock (1971) mentioned that a captive neonate swallowed a conspecific neonate that was dead or nearly so. Klauber (1972) included a field observation of an adult swallowing a conspecific two-thirds its length. Powers (1972) noted that a captive adult had consumed a dead conspecific and subsequently regurgitated it. Lillywhite (1982) reported the consumption (twice) of a decomposing juvenile by a conspecific juvenile in captivity. A field-caught 842 mm (total length?) female contained a 264 mm juvenile folded in half (Genter, 1984). He noted there was little decomposition but could not tell if the juvenile was eaten as carrion or was killed by the female.

Crotaphopeltis hotamboeia - An x-ray photograph in Rose (1962) shows a captive juvenile with the remains of a conspecific in its stomach. The cannibal regurgitated it several days later, then ate it again.

Dendroaspis viridis - adult-adult, in captivity: Cansdale (1961).

Diadophis punctatus - adult-adult, in captivity: Rosenberg (1980). A 610 mm total length captive(?) swallowed a 483 mm conspecific and later disgorged it (Cunningham, 1959). An adult male 275 mm SVL from North Carolina died in the act of eating a 185 mm conspecific male and was preserved by W. H. Martin. The event occurred in the collecting bag after separate collections

Dinodon semicarinatus - Mishima (1966) noted that a field-collected 2010 mm (total length?) adult contained a 360 mm conspecific.

Dispholidus typus - Rose (1954) encountered an adult consuming a dead conspecific from which maggots were dropping. FitzSimons (1962) and Broadley (1983) reported that cannibalism is not unknown and there are known cases of boomslangs swallowing conspecifics of nearly equal size.

Dryophis mycterizans - Ferguson (1895) noted that a captive snake had consumed half of another while both were trying to eat the same prey item.

Duberria lutrix - no specific information, field: Pitman (1974). Broadley (1959) mentioned that six young were eaten by adults in captivity.

Echis carinatus - adult-adult, in captivity: Millard (1906); no specific information, field: Bogdanov (1965); no specific information, in captivity: Pit-

man (1974). Duff-Mackay (1965) described head biting and swallowing by captive adults, but only a few were eaten whole. He postulated that reduced resource levels induced this behavior.

Elaphe carinata - Pope (1935) recorded that a 727 mm adult ate a 468 mm juvenile in the field.

Elaphe dione - no specific information, field: Bogdanov (1965).

Elaphe guttata - juv.-juv., in captivity: Hillis (1974); juv.-juv., in captivity: Ippoliti (1980); adult-juv., in captivity: C. M. Craig (pers. comm.). Cannibalism is regularly observed in captive juveniles, especially after their return to communal rearing cages after separate feeding (R. E. Honegger, pers. comm.).

Elaphe obsoleta - juv.-juv., in captivity: Damm (1977); adult-juv., in captivity: C. M. Craig (pers. comm.); adult-adult, in captivity: J. W. Steiner (pers. comm.).

Elapsoidea semiannulata - juv.-juv., in captivity: Broadley (1971).

Epicrates striatus - Hanlon (1964) mentioned that a captive female ate, after apparently killing, at least two of her offspring. Huff (1980) observed a captive parturient female eating fetal membranes, dead young and one live neonate.

Hydrodynastes gigas - juv.-juv., in captivity: R. E. Honegger (1984, pers. comm.).

Lampropeltis calligaster - Smith (1961) reported that a recently captured adult regurgitated an equally large conspecific.

Lampropeltis getulus - no specific information, in captivity: C. M. Craig (pers. comm.). An adult kingsnake swallowed an adult conspecific when both tried to eat the same blacksnake (Anonymous, 1892). Corrington (1929) noted that kingsnakes readily ate their own kind. An approximately 1000 mm captive adult ate a cagemate about 100 mm smaller (Daniel, 1948).

Lampropeltis triangulum - adult-juv., in captivity: Dyrkacz (1977); juv.-juv., in captivity: Miller and Grall (1978). Skehan (1960) reported that a 1082 mm specimen regurgitated a 210 mm juvenile the day after field capture. Rothman (1961) described a captive specimen which preferred to eat conspecifics over other snake prey offered. Fitch and Fleet (1970) reported a captive adult partially consuming a conspecific adult while both were consuming a prey item.

Leptodeira albofusca - adult-adult, in captivity: Peters (1955).

Leptodeira annulata - adult-juv., in captivity: Wehekind (1955); adult female-adult male, in captivity: Petzold (1969).

Lycophidion capense - A 480 mm total length captive female ate a similar-sized male (D. G. Broadley, pers. comm.).

Malpolon moilensis - no specific information, field: Vernet and Grenot (1972).

Masticophis flagellum - adult-(?), field: Guidry (1953); no specific information, in captivity: Cunningham (1959); adult-adult, in captivity: Tennant (1984); adult-adult, in captivity: J. Stout (pers. comm.).

Masticophis taeniatus - no specific information, field: Parker and Brown (1980).

Mehelya capensis - no specific information, unknown: Sweeney (1961).

Mehelya stenophthalma - no specific information, unknown: Pitman (1974). FitzSimons (1962) and Broadley (1983) note that this species is cannibalistic in its feeding habits, showing a marked preference for other snakes.

Micrurus corallinus - Hoge and Federsoni (1981) illustrate a specimen with the tail of a conspecific protruding from its mouth.

Micrurus fulvius - Loveridge (1938) reported that a 622 mm SVL male captured in the field regurgitated a 440 mm conspecific and an *Ophedrys aestivus*. He later (Loveridge, 1944) found a 620 mm male which had eaten a 535 mm male. A road-kill 429 mm male contained another male (178 mm) and a 186 mm *Storeria dekayi*; both were probably trying to eat the same prey item (Curtis, 1952). Chance (1970) found a 203 mm total length juvenile in the stomach of a field-collected 762 mm adult. Jackson and Franz (1981) synthesized these observations in a review of the ecology of this species. Greene (1984) reported the following combinations for the species: adult male-adult male (2), adult male-adult gravid female, adult female-adult female, adult male-juv. male.

Micrurus ibiboboca - no specific information, unknown: Amaral (1933).

Micrurus lemniscatus - adult-juv., field: Wehekind (1955).

Micrurus psypes - no specific information, unknown: Roze (1983). No specific information, unknown: Wehekind (1955); reported as *M. corallinus*.

Naja haje - adult male-adult male, in captivity: G. Carl (pers. comm.); adult-juv., in captivity: D. G. Broadley (pers. comm.).

Naja melanoleuca - no specific information, unknown: Pitman (1974). An x-ray of a juvenile which had consumed a juvenile cagemate is in Dolensek and Burn (1985).

Naja mossambica - juv.-juv., in captivity: D. G. Broadley (pers. comm.).

Naja naja - adult-adult, in captivity: Mahendra (1931); juv.-juv., in captivity: Olexa (1975); adult female-adult male, in captivity: Petzold and Engelmann (1975). Millard (1902) mentioned a captive black cobra which had eaten a cagemate while both tried to eat a frog. Deraniyagala (1955) noted that a 1890 mm field-caught specimen had swallowed another 1430 mm in length. The victim had numerous fang marks on the head and neck and a 75 mm wound middorsally.

Naja nivea - no specific information, unknown: FitzSimons (1962).

Nerodia sipedon - adult male-juv., in captivity: Anonymous (1892); adult-juv., field: Conant (1938); no specific information, field: Uhler, et al. (1939). A photograph in Neill (1968) shows a captive adult attempting to swallow two conspecific adults who were all trying to swallow the same prey item.

Ophedrys aestivus - William W. Lamar (pers. comm.) noted that a captive adult consumed another when both tried to eat the same cricket. A captive female which had just laid her eggs ate a gravid conspecific female slightly smaller than herself (deRageot, 1964).

Ophiophagus hannah - Evans (1902) reported a field observation of a 3.45 m king cobra capturing, killing and swallowing an 2.59 m conspecific. Smith (1943) noted that king cobras were not adverse to eating their own kind.

Philothamnus irregularis - adult-adult, in captivity: Pitman (1974).

Pituophis melanoleucus - no specific information, unknown: Miller and Stebbins (1964). Klauber (1947) reported a road-kill *P. m. annectans* which contained a conspecific "almost as large". Wellstead (1981) described an adult male on a road apparently attempting to eat an injured adult male conspecific. He suggested the attempt was a natural response to the scent of a recently eaten gopher on the head of the injured snake.

Polemon christy - Pitman (1974) noted that small individuals are killed (and eaten?) by larger ones.

Pseudoboa coronata - no specific information, unknown: Wehekind (1955), this species does not occur on Trinidad (W.W. Lamar, comm.).

Pseudoboa neuwiedi - no specific information, unknown: Wehekind (1955).

Ptyas mucosus - no specific information, field (?): Wall (1904, 1906); no specific information, field: Bogdanov (1965); adult-adult, in captivity: Whitaker (1970). Ferguson (1895) described a captive rat-snake eating a conspecific while both tried to consume a frog.

Python sebae - no specific information, in captivity: Roule (1926).

Python molurus - Millard (1902) noted that a 2.74 m adult ate a cagemate (size unknown) while both tried to eat a partridge. Acharjyo and Misra (1976) noted that 17 of 38 captive hatchlings were "accidentally" eaten by conspecifics, while "attacking" each other.

Rhabdophis tigrinus - A captive 752 mm SVL female ate a 570 mm male and both subsequently died (Moriguchi, 1981).

Sanzinia madagascariensis - A captive female ate a Siamese twin neonate after its birth (Jes, 1984).

Sistrurus catenatus - Ruthven (1911) reported the consumption of a conspecific which had apparently been dead for some time. Klauber (1972) noted that one massasauga ate a conspecific while both were attempting to eat the same prey.

Sistrurus miliarius - no specific information, unknown: Allen and Neill (1950).

Thamnophis elegans - Fox (1952) mentioned these snakes may lunge at each other in a feeding frenzy and large ones may swallow small ones. White and Kolb (1974) found 190-200 mm SVL juveniles in the stomachs of field-collected adults of 460-560mm SVL. Carl R. Peterson (pers. comm.) palped a 280 mm SVL (9 g) *T. elegans* out of a field-collected 490 mm (41 g) adult male. He noted that the prey had been doubled over and swallowed mid-body first. Stevan J. Arnold (pers. comm.) noted that in the approximately 400 garter snakes he examined, only 2 instances of cannibalism were recorded.

Thamnophis sauritus - adult-juv., in captivity: Smith (1961). Duellman (1948) reported that a 731mm female ate five of her offspring in captivity.

Thamnophis sirtalis - adult-juv., field: R. Scudder (pers. comm.). Hamilton (1951) found seven young of approximately equal size beneath a slab of wood; one had eaten a conspecific of nearly equal size. A captive hatchling garter snake from Pennsylvania (Carnegie Museum of Natural History,

CM 91716) was preserved in the process of eating a conspecific litter mate. The prey was doubled over and swallowed mid-body first. Schwartz (1985) described aggression and the killing and partial consumption of a 134 mm SVL male by a 133 mm SVL female in captivity.

Thelotornis capensis - Donald G. Broadley (pers. comm.) recorded several instances of captive adults swallowing other adults when both tried to swallow the same lizard or frog from opposite ends.

Thelotornis kirtlandi - no specific information, in captivity: Wilson (1965). Sweeney (1961) noted that a 1290 mm female ate a conspecific 75 mm longer than itself.

Tropidoclonion lineatum - no specific information, unknown: Ramsey (1953).

Tropidophis haetianus - adult-adult, in captivity: R. I. Crombie (pers. comm.).

Trimeresurus flavoviridis - Koba (1979) recorded eight conspecifics in the stomachs of a sample of 63 field-collected specimens.

Trimeresurus trigonocephalus - adult female-adult male, in captivity: H. Quinn (pers. comm.).

Unechis gouldii - Shine (1977) recorded a single conspecific in a sample of 15 field-caught specimens.

Vipera ammodytes - adult-juv., field: Bolkay (1923), Beskov and Nankinov (1979), Street (1979) and Biella (1983). Stanic (1966) contains a photograph and an x-ray of an adult which had consumed a conspecific in captivity.

Vipera aspis - no specific information, in captivity: Naulleau (1968). Cannibalism occurred when prey was introduced and the snakes became over-excited (Naulleau, 1973a).

Vipera lebetina - Petzold and Budich (1972) mentioned a captive adult which swallowed another after both struck and ate the same prey item.

Vipera russellii - juv.-juv., in captivity: Whitaker (1971, 1978); adult-juv., in captivity: Gerlach (1971); juv.-juv., in captivity: Glenn, et al. (1975).

Vipera ursinii - adult-juv., in captivity: Vasarhelyi (1965, in Street, 1979).

Waglerophis merremii - no specific information, in captivity: Lavilla, et al. (1979). Hermann (1921) noted that a captive specimen ate a smaller conspecific when both tried to eat the same frog.

Testudinata

Chelydra serpentina - adult-juv., in captivity: M. C. Nowak (pers. comm.). One field-collected specimen contained a conspecific in its stomach (Lagler, 1943).

Chrysemys picta - adult-juv., field(?): Wilbur (1975).

Clemmys muhlenburgii - no specific information, unknown: Arndt (1972).

Podocnemis vogli - Pritchard and Trebbau (1984) noted that evidence of cannibalism was found by Ramo (1980) in a survey of stomach contents.

Sternotherus minor - Ernst and Barbour (1972) noted that a captive juvenile killed and partially ate two other juveniles.

Terrapene carolina - adult-juv., in captivity: W. B. Love (pers. comm.).

Terrapene ornata - adult-juv., unknown: Ernst and Barbour (1972).

Trionyx sinensis - adult-juv., unknown: Ernst and Barbour (1972). Chen (1976) noted that juveniles are eaten by adults in aquaculture ponds.

Crocodylia

Alligator mississippiensis - adult-juv., unknown: Reese (1915). Kellogg (1929) included F. M. Uhler's observations of a captive 2.1 m adult swallowing a 1.1 m juvenile, noting that crushing of the bones could be heard. He also noted that other alligators have been known to eat juveniles. Schmidt and Inger (1957) stated that adults eat a large proportion of the young of their own species. Neill (1971), however, stated that cannibalism is rare in alligators and that its occurrence probably reflects carrion-eating. He also said the presence of alligator scales in stomachs should be interpreted as being used for gastroliths, rather than an indication of cannibalism.

Caiman crocodilus - Staton and Dixon (1975) witnessed cannibalism on two occasions by adult males on 400-500 mm SVL juveniles and included a photograph of one of the juveniles taken from a male. They noted the high mortality rate of hatchlings was probably due to cannibalism under high density situations in small ponds created during the dry season. Two conspecifics were recorded in the diet of this species by Schaller and Crawshaw (1982) in southwestern Brazil.

Crocodylus moreleti - Cott (1961) mentioned that adults were known to eat juveniles. Hunt (1977) observed adults preying on juvenile conspecifics under captive conditions.

Crocodylus niloticus - Cott (1961) recorded 17 conspecifics in the stomachs of adult crocodiles and included reports of two other instances. Most victims were juveniles and Cott stated that cannibalism by older crocodiles is an important factor in juvenile mortality. Neill (1971) was especially critical of Cott's statements that the secretive behavior of juveniles was a result of cannibalism by adults.

Osteolaemus tetraspis - Tryon (1980) described a captive adult male eating an inviable (dead?), deformed hatchling, and a female which swallowed a dead neonate after she had broken the egg.

Paleosuchus palpebrosus - Medem (1981) mentioned that adults will consume smaller individuals on occasion.

Paleosuchus trigonatus - Medem (1981) noted for this species that adults will sometimes eat smaller individuals.

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